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Possible Stock Structure of Coastal Bottlenose Dolphins off Baja California and California Revealed by Photo-Identification Research

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Abstract.—Boat-based photo-identification research has been carried out on bottlenose dolphins in eastern North Pacific coastal waters off northern Baja California, Mexico and southern and central California, USA from 1981 to 2001. Within these waters, bottlenose dolphins routinely travel back and forth between coastal locations while generally staying within a narrow corridor extending only 1–2 km from the shore. Inter-area match rates for 616 dolphins photo-identified between 1981–2000 in four California coastal study areas (CCSAs) of Ensenada, San Diego, Orange County and Santa Barbara averaged 76%. To explore possible southern range limits for these dolphins, photo-identification surveys were carried out in the coastal waters off San Quintín, Baja California, Mexico between April-August 1990 ($n=8$ surveys) and July 1999 to June 2000 ($n=12$ surveys). The 207 individual dolphins identified off San Quintín were compared to the 616 dolphins identified in the CCSAs. The inter-area match rate between San Quintín and the CCSAs was 3.4% ($n=7$ dolphins). This low rate contrasts sharply with the much higher average match rate of 76% observed between the CCSAs. These differences in match rates suggest that both a California coastal stock and coastal Northern Baja California stock may exist, with only a limited degree of mixing between them.

The common bottlenose dolphin (*Tursiops truncatus*) is the most frequently encountered cetacean in the nearshore waters of California and Baja California, Mexico. Two distinct bottlenose dolphin ecotypes occur in these waters: a coastal form that is typically found within 1–2 km of shore (Carretta et al. 1998; Defran and Weller 1999;

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Bearzi 2005) and an offshore form that is distributed in deeper waters, typically greater than a few kilometers from shore (Defran and Weller 1999; Bearzi et al. 2009). Differentiation of these two ecotypes, which are managed as separate stocks by the National Marine Fisheries Service (Carretta et al. 2013), is supported by morphological (Walker 1981; Perrin et al. 2011), photographic (see Shane 1994) and genetic data (Lowther-Thieleking et al. 2014).

The California coastal stock is small, estimated to contain about 450–500 individuals (Dudzik et al. 2006; Carretta et al. 2013) that are distributed between Monterey, California and Ensenada, Baja Mexico (Defran et al. 1999; Hwang et al. 2014), with occasional sightings as far north as San Francisco, California[1]. Photo-identification research has been carried out on the coastal stock off California, and to a lesser extent off Northern Baja California, since the early 1980s. Areas off California and Baja California where photographic data have been collected include: (1) Ensenada, (2) San Diego, (3) Orange County, (4) Santa Monica Bay, (5) Santa Barbara, (6) Monterey Bay and (7) San Francisco Bay (Fig. 1). In general, photo-identification data have shown that California coastal dolphins display little site fidelity to any portion of their distribution (Defran et al. 1999; Hwang et al. 2014). Instead, they routinely travel back-and-forth within their range, on some occasions in excess of 900 km, while at the same time typically staying very near shore (Defran et al. 1999; Hwang et al. 2014).

Records from the nineteenth century suggest that coastal bottlenose dolphins may have once occurred in Monterey Bay and San Francisco Bay (Dall 1873; True 1889; Orr 1963). More recent studies, however, considered the northern range boundary to be located off Los Angeles County up until the early 1980s (Norris and Prescott 1961; Dohl et al. 1981; Leatherwood and Reeves 1982). The 1982-83 El Niño Southern Oscillation (ENSO) dramatically impacted the coastal marine ecosystem off California and Baja. It was during this ENSO event that California coastal stock dolphins extended their northern range back to Monterey Bay (Wells et al. 1990). This northern range extension has persisted to the present day (Riggin and Maldini 2010; Maldini et al. 2010; Cotter et al. 2011) and now extends even further north to San Francisco Bay and most recently, Bodega Bay[1].

The southern boundary of the California coastal stock is less well known but photo-identification data demonstrate that it extends to at least Ensenada (Defran et al. 1999; Hwang et al. 2014). In this research, boat-based photo-identification surveys of coastal bottlenose dolphins were carried out south of Ensenada off San Quintín Bay, Baja California (Figs. 1 & 2). The goal of this research was twofold: (1) to examine the degree of overlap between coastal dolphins photo-identified off San Quintín and those photo-identified in study areas off Ensenada, San Diego, Orange County, and Santa Barbara, and (2) to use photo-identification data to determine if the southern range of the California coastal stock extended as far south as the San Quintín area.

Methods

The general design used in this study was the same as our earlier studies that compared independently collected bottlenose dolphin photo-identification catalogs from California and Baja California (Defran et al. 1999; Hwang 2014).

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Fig. 1. Coastal locations where California coastal stock bottlenose dolphins have been photo-identified. Point Conception and Punta Colonet are included to indicate the northern and southern coastal boundaries of the Southern California Bight. Study areas marked with an asterisk indicate those that were compared to San Quintín sightings (Table 1).

Study Area

This study was conducted in the coastal waters south of San Quintín Bay, Baja California, during two independent study periods: 1) April, June and August 1990, $n=8$ surveys (Caldwell 1992); and 2) July 1999 to June 2000, $n=12$ surveys (Morteo et al. 2004). The San Quintín study area was located approximately 376 km south of San Diego and about 200 km south of Ensenada. Within the study area, the survey track extended

Fig. 2. San Quintín study area. Dashed line indicates photo-identification survey route.

32 km southward from a point 8 km east of Azufre Point (30°23'50" N; 115°54'42" W) south to Rosario Canon (30°09'06" N; 115°48'27" W) (Fig. 2). Most surveys in 1990 began at the Base Camp near El Socorro and extended 18 km south to Rosario Canon. During the 1999–2000 study period, surveys began about 8 km east of Azufre Point and extended 26 km south to Hondo Creek (Fig. 2).

Photo-Identification Surveys and Photographic Data Analysis

Survey methodology and photo-identification analysis procedures employed during both study periods in San Quintín followed those used previously in the Ensenada, San Diego, Orange County and Santa Barbara study areas, hereafter referred to as California coastal study areas (CCSAs). Detailed descriptions of these procedures are provided

Table 1. Summary information on survey effort, study period, photographic data, and data sources for all study areas[a].

Study area	Number of surveys (complete, partial)	Study period	Number of dolphins identified
San Quintin	20 (20, 0)	1990[1], 1999–2000[2]	207
Ensenada	23 (23, 0)	1985–1986[3], 1999–2000[4]	129
San Diego	241 (157, 84)	1981–1989[5], 1996–1999[6&7]	518
Santa Barbara	73 (55, 18)	1987 & 1989[3], 1998–1999[7]	213

Data sources: [1] Caldwell (1992), [2] Morteo et al. (2004), [3] Defran et al. (1999), [4] Guzón-Zatarain (2002), [5] Defran and Weller (1999), [6] Dudzik (1999), [7] Lang (2002). [a] Some numbers differ from those given in original data sources due to refinement and revision of the dataset over time and the elimination of sightings not meeting the specified photographic quality criteria.

elsewhere (Caldwell 1992; Defran and Weller 1999; Defran et al. 1999; Dudzik 1999; Lang 2002; Morteo et al. 2004) but are briefly described here. Photographic surveys involved slow travel in small boats while moving parallel to the coast and outside the surf line; generally within 500–750 m of shore and corresponding to water depths between 4 m to 10 m. Surveys were conducted in sea state and visibility conditions adequate for finding and photographing dolphins. Although past data demonstrated that most coastal bottlenose dolphins are typically found within 500 m of the shore (Hanson and Defran 1993; Defran and Weller 1999; Bearzi 2005; Carretta et al. 2013), two or more observers, nevertheless, visually searched the area from the shore to ~ 2 km offshore to ensure complete coverage of coastal waters. Once a group of dolphins was sighted, initial estimates of group size, as well as information on time, location, environmental conditions and behavior were recorded.

Following initial estimates of group size, the survey vessel maneuvered to a distance from the dolphins suitable for photo-identification. Thirty-five millimeter SLR film cameras equipped with telephoto lenses were used to photograph all dolphins (marked and unmarked) within a group. Initial estimates of group size were revised as necessary, and contact with the group was maintained until photographic effort was completed, or dolphins began exhibiting avoidance behavior. Identical procedures were repeated as the vessel resumed travel on the predetermined survey route and as additional dolphin groups were encountered.

The best quality photograph of every dolphin was scanned and converted into a high-resolution digital image. Of these, only high quality photographs of dorsal fins with two or more distinctive dorsal fin notches were used for analysis. Distinctive dorsal fins were those that had sufficient notching on the leading or trailing edge such that they could be matched to high quality dorsal fin photographs from other sightings (Urian and Wells 1996; Defran and Weller 1999; Defran et al. 1999; Mazzoil et al. 2004). Only unambiguous matches were accepted as resightings (i.e., a re-identification of a previously identified individual). Dorsal fin images from selected CCSAs (marked with an asterisk in Fig. 1) were analyzed and maintained in the Cetacean Behavior Laboratory at San Diego State University. The combined photo-identification catalog for the CCSAs consisted of 616 individuals identified during two sample periods: (1) 1981 to 1989, and (2) 1996 to 2000. Table 1 provides a summary of survey effort, study period, photographic data and data sources for each of the CCSAs.

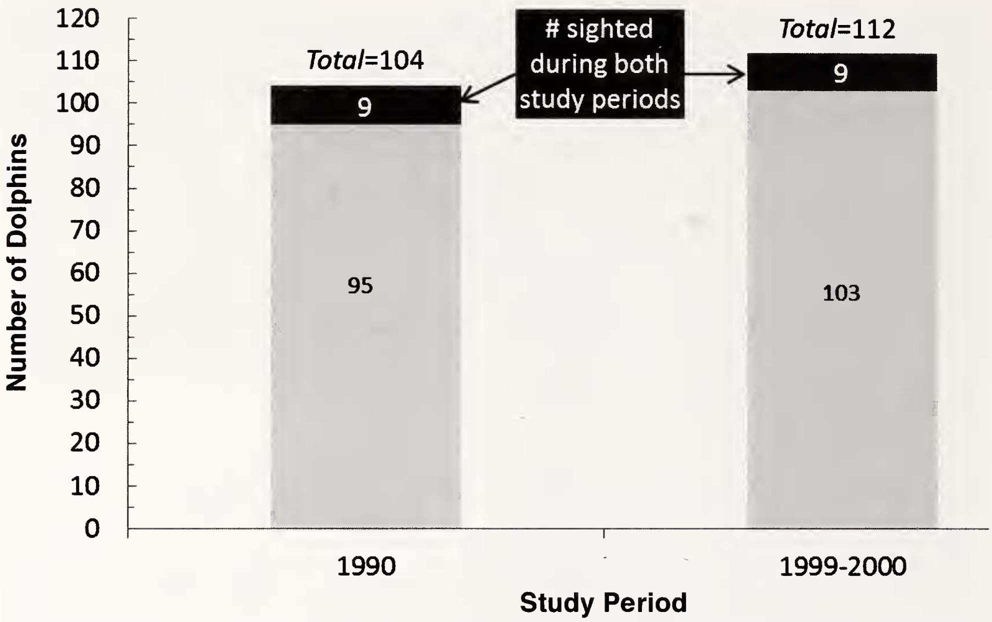

Fig. 3. Number of dolphins identified during the 1990 and the 1999–2000 San Quintín study periods. Some dolphins (n=9) were sighted during both study periods, otherwise individuals were sighted only during the indicated study period.

Results

During the 1990 and 1999–2000 study periods in San Quintín, 104 and 112 individuals were identified, respectively. Nine dolphins were identified in both the 1990 and 1999–2000 study periods while 95 of these individuals were sighted only during 1990 and 103 only in 1999–2000. The combined number of individuals identified in San Quintín during both study periods was 207 (Fig. 3). During the 1990 and 1999–2000 study periods, most individuals were sighted only one time; but some individuals were sighted on multiple occasions within a respective study period (Fig. 4).

Inter-study area match rates (MR) were derived by calculating the percent of individuals photographed in one study area, such as in San Quintín, that were also photographed in another study area. Similar match rate calculations were made for individuals photographed within the different CCSAs. The first comparison involved a composite of inter-study area matches reported for the two sampling periods when data were collected in the CCSAs: 1981–1989 (Defran et al. 1999) and 1996–2000 (Hwang et al. 2014) (Table 1). Match rates for the 1981–1989 sample were calculated by comparing the percent of dolphins identified in Ensenada (n=68, MR=88%), Orange County (n=133, MR=92%) and Santa Barbara (n=43, MR=88%) that matched to dolphins identified in San Diego (n=404) where the sample size was highest. Match rates for the 1996–2000 sample were calculated by comparing the percent of dolphins identified in Ensenada (n=81, MR=43%) and Santa Barbara (n=182, MR=67%) that matched to San Diego (n=292) where the sample size was again the highest. The combined 1981–1989 and 1996–2000 average match rate for the CCSAs was 76% (±18.5 S.D.).

The second comparison involved the inter-study area match rates between dolphins identified off San Quintín with dolphins in the combined 1981–1989 and 1996–2000 CCSAs catalog. Inter-study area matches occurred between both San Quintín datasets and

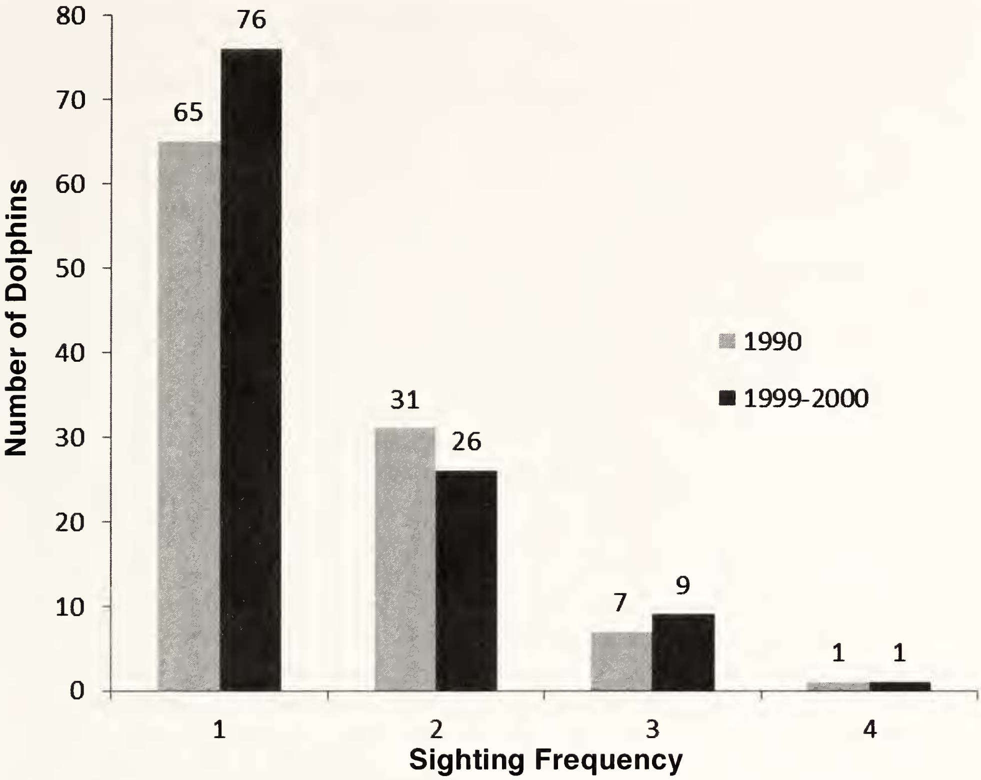

Fig. 4. Sighting frequency of dolphins during the 1990 and 1999–2000 San Quintín study periods.

the CCSAs catalog. In the 1990 San Quintín sample, 2 of the 104 dolphins identified were matched (MR=1.9%) to the combined CCSAs catalog. In the 1999–2000 San Quintín sample, 5 of the 112 dolphins identified were matched (MR=4.5%) to the combined CCSAs catalog. When dolphins identified off San Quintín in 1990 and 1999–2000 were combined (n=207), 7 (MR=3.4%) were matched to dolphins in the CCSAs catalog.

Finally, 3 of the 7 dolphins matched between San Quintín and the CCSAs catalog were sighted in at least one of the CCSAs before and after their sighting(s) in San Quintín. The first of these dolphins was sighted before and during the 1990 San Quintín study period and again during the 1996–2000 CCSAs study period. The other two dolphins were sighted after the 1996–2000 CCSAs study period, during more recent surveys conducted in the San Diego study area between 2004–2011 (unpublished data, D. Weller). Of these seven matches, all were sighted in San Diego, two were also sighted in Ensenada, and two were also sighted in Orange County.

Discussion

Identifying population stock boundaries is important for management purposes in that it allows for a range-wide evaluation of potential threats. With such management considerations in mind, the most significant finding of this research was the low overlap (MR=3.4%) for dolphins photographed off San Quintín and those photographed in one or more of the CCSAs. In comparison, the overall match rate was considerably higher (MR=76%) between CCSAs study sites. These match rate differences suggest that both a California coastal stock and Northern Baja California coastal stock exist, with only a limited degree of mixing between them.

Results from within the time frame of this research (i.e., 1990–1999) suggest that the northern range boundary for the proposed coastal Northern Baja stock is located somewhere between San Quintín and Ensenada. Although most individuals identified off San Quintín were sighted only once, the small number of individuals that were sighted multiple times within a given survey period provides some evidence for at least short-term use of the area. Similarly, the nine dolphins sighted during both San Quintín study periods indicate some degree of longer-term use of the area.

While the low match rate between San Quintín and the CCSAs suggests a small degree of overlap between the two proposed stocks, the total number of surveys conducted off San Quintín (n=20) was relatively low in comparison to the number of surveys conducted in some of the CCSAs. That being noted, the number of surveys conducted off San Quintín (n=20) is similar to the number of surveys off Ensenada (n=23) that were also conducted during two distinct time periods that overlapped or nearly overlapped with the timing of the San Diego surveys. In this case, match rates for the Ensenada to San Diego photo-identification comparisons were markedly higher (MR=88% during 1981–1989; MR=43% during 1996–2000) than those found for the comparison of the CCSAs catalog with the two San Quintín survey periods (i.e., 1.9% and 4.5%, respectively). Further, while the number of San Quintín surveys was lower than those in the San Diego and Santa Barbara study areas, the number of dolphins identified was quite high. By way of comparison, the 207 individuals identified (sampled) in San Quintín was greater than the sample size in Ensenada (Table 1., n=129) and comparable to the total number of individuals in the Santa Barbara sample (Table 1., n=213). Thus, it is unlikely that the 3.4% inter-area match rate between San Quintín and the CCSAs is related to low survey effort or small sample sizes in San Quintín.

The primary variables contributing to the proposed stock structure are as yet unknown. Oceanographic and bathymetric variables have been hypothesized as potential habitat barriers for coastal bottlenose dolphins off California and Baja California (Caldwell, 1992) but verification of these mechanisms is unresolved. When stock separation occurs in bottlenose dolphins in the absence of confirmed geographic barriers, as is the case along the eastern North Pacific coastline (this research), as well as along the western North Atlantic Seaboard and within the northern inshore areas of the Gulf of Mexico (e.g., Texas, Florida), social structure, prey availability, and foraging specialization have been cited as possible foundations for dispersal tendencies (Sellas et al. 2005; Rosel et al. 2009; Toth et al. 2011). Such stock distinctions may be useful for management purposes, even when there is a moderate level of mixing with other adjacent stocks, such as that which occurs within Sarasota Bay and between nearby Gulf of Mexico inshore areas of Tampa Bay and Charlotte Harbor (see reviews in Selas et al. 2005; Rosel et al. 2009).

Complex social structure may act to minimize dispersal due to the investment required to build and maintain social bonds (Rosel et al. 2009). Social affiliations among California coastal dolphins, however, are highly dynamic (Weller 1991). Dispersal may also be limited in areas that have consistently high prey densities, allowing a population to be sustained long-term within a limited range. However, the regular travel of California coastal dolphins within their range suggests a patchy distribution of prey species requiring frequent relocation (Weller 1991; Hanson and Defran 1993; Defran et al. 1999; Ogle 2005; Hwang et al. 2014).

Among the inshore bottlenose dolphins found in some Atlantic Seaboard and Gulf of Mexico areas, as well as within Shark Bay, Australia, a number of foraging and resource specializations have developed. Over time, such specializations as strand feeding, sponge feeding and confinement to shallow water bays and estuaries for shark avoidance, could result in geographic range restrictions that give rise to stock separation (Silber and Fertl 1995; Connor et al. 2000; Sellas et al. 2005; Mann et al. 2008; Rosel et al. 2009). Similar mechanisms that might restrict the range of California coastal dolphins have not been observed.

Examination of the sighting records for the seven dolphins identified in both San Quintín and at least one of the CCSAs suggests that the mixing for some of these seven dolphins may not represent permanent immigration of California coastal dolphins into the putative coastal Northern Baja stock. Three of these seven dolphins were seen in at least one of the CCSAs both before and after their sightings in San Quintín. Thus, these dolphins appear to have visited San Quintín but subsequently returned to their putative range within the CCSAs. It is unknown whether such visits entail exploratory movements in search of prey and/or if they represent a mechanism by which some gene flow between the two stocks could be occurring. A final point relates to the 3.4% match rate reported in this research. The similarly low match rates observed for the two San Quintín sample periods (i.e., 1990=1.9%, 1999–2000=4.5%) suggests that the degree of mixing does fluctuate, at least to a small degree. Additional research conducted over years and varying oceanic conditions could provide a more sensitive measurement of dolphin mixing between the San Quintín and Southern California Bight study areas.

Thus far, the proposed stock separation presented herein relies entirely on photo-identification data. The differentiation of California coastal ecotype bottlenose dolphins from the offshore ecotype has successfully relied on the multiple data types and sources, including analyses of morphology, microbiology and genetics, as well as photo-identification (Walker 1981; Perrin et al. 2011; Bearzi et al. 2009; Lowther-Thieleking et al. 2014). Among these multiple data sources, genetic analyses have been particularly revealing in efforts to define and differentiate the coastal and offshore bottlenose dolphin stocks within California waters (Lowther-Thieleking et al. 2014), as well as in numerous other regions (Sellas et al. 2005; Rosel et al. 2009; Waring et al. 2012). Similar genetic data are needed, but remain to be collected from San Quintín coastal dolphins. Once such data are available, a genetic comparison to the California coastal stock can be made (Lowther-Thieleking et al. 2014). Combining genetic comparisons with future photo-identification data would provide a broader and more informed foundation from which management decisions can be made with regard to coastal bottlenose dolphins off California and Baja California.

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